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Underwater audiograms are available for only a few odontocete species. A false killer whale (*Pseudorca crassidens*) was trained at Sea Life Park in Oahu, Hawaii for an underwater hearing test using a go/no-go response paradigm. Over a 6-month period, auditory thresholds from 2–115 kHz were measured using an up/down staircase psychometric technique. The resulting audiogram showed hearing sensitivities below 64 kHz similar to those of belugas (*Delphinapterus leucas*) and Atlantic bottlenosed dolphins (*Tursiops truncatus*). Above 64 kHz, this *Pseudorca* had a rapid decrease in sensitivity of about 150 dB per octave. A similar decrease in sensitivity occurs at 32 kHz in the killer whale, at 50 kHz in the Amazon River dolphin, at 120 kHz in the beluga, at 140 khz in the bottlenosed dolphin, and at 140 kHz in the harbor porpoise. The most sensitive range of hearing was from 16–64 kHz (a range 10 dB from the maximum sensitivity). This range corresponds with the peak frequency of echolocation pulses recorded from captive *Pseudorca*. Keywords: ...; marine biology; (KT)

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Underwater audiogram of a false killer whale (*Pseudorca crassidens*)

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Underwater audiograms are available for only a few odontocete species. A false killer whale (*Pseudorca crassidens*) was trained at Sea Life Park in Oahu, Hawaii for an underwater hearing test using a go/no-go response paradigm. Over a 6-month period, auditory thresholds from 2–115 kHz were measured using an up/down staircase psychometric technique. The resulting audiogram showed hearing sensitivities below 64 kHz similar to those of belugas (*Delphinapterus leucas*) and Atlantic bottlenosed dolphins (*Tursiops truncatus*). Above 64 kHz, this *Pseudorca* had a rapid decrease in sensitivity of about 150 dB per octave. A similar decrease in sensitivity occurs at 32 kHz in the killer whale, at 50 kHz in the Amazon River dolphin, at 120 kHz in the beluga, at 140 kHz in the bottlenosed dolphin, and at 140 kHz in the harbor porpoise. The most sensitive range of hearing was from 16–64 kHz (a range 10 dB from the maximum sensitivity). This range corresponds with the peak frequency of echolocation pulses recorded from captive *Pseudorca*.

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INTRODUCTION

False killer whales (*Pseudorca crassidens*) are toothed whales that inhabit temperate and tropical waters of the Atlantic and Pacific oceans. They are highly social, sometimes found in groups of nearly 100 animals (Leatherwood *et al.*, 1982). They are pelagic, more commonly found in deep water than near land, and eat large fish and squid. They produce whistles and pulses (Watkins, 1980; Busnel and Dziedzic, 1968). We know little about their sensory abilities, except for a preliminary study by Thomas *et al.* (in press) that indicates they echolocate.

Underwater behavioral audiograms are available for only a few odontocete species: *Phocoena phocoena* (Andersen, 1970), *Inia geoffrensis* (Jacobs and Hall, 1972), *Tursiops truncatus* (Johnson, 1967), *Delphinapterus leucas* (White *et al.*, 1978), and *Orcinus orca* (Hall and Johnson, 1971). All have the typical U-shaped mammalian hearing curve. Low-frequency hearing among these species is comparable, but the high-frequency cutoff is species specific.

Our objectives were to: (i) collect a behavioral underwater audiogram of a false killer whale; (ii) compare our results with those from other odontocetes; and (iii) relate the range of most sensitive hearing to the peak frequency of echolocation pulses from *Pseudorca*.

I. METHODS

A. Subject

An adult male false killer whale, "I'a nui hahai," was the test subject. This animal weighed approximately 700 kg, was about 4.5 m in length, and had been in captivity at Sea Life Park in Hawaii since 1974. Even though the whale was at least 18 years old, we believe that its hearing is normal. Medical records showed no evidence of ototoxic medication. The animal always lived in large quiet pools with skimmer filter systems that do not require pumps. It was tested once per day from June–December 1986, in addition to the three to five shows it performed. The animal's daily intake was about 25 kg of smelt and herring, of which 5 kg was used during threshold tests.

B. Apparatus

We conducted the study at Whaler's Cove Theater at Sea Life Park in Oahu, Hawaii. In this theater, a replica of a sailing ship separates the main pool from a holding pool. Tests took place in the holding pool, which is irregular in shape with maximum dimensions of 15 m(l) × 7 m(w) × 4 (depth) m. The ship supported a retractable aluminum plank (Fig. 1), which served as the trainer's platform, animal's station, and support for signal projection equipment. The whale stationed on the crooked portion between the vertical legs of the plank (1 m below water). When in the proper stationing position, the animal rested its thorax on the crook, with the leading edge of its flippers against the crossmember (A in Fig. 1). The underwater transducer for projecting test signals was suspended from the plank at 3.2 m from the crook (B in Fig. 1). Two underwater lights mounted in the ship (one on each side of the transducer) faced the animal when it was at station (C in Fig. 1).

We measured the ambient pool noise and the received sound-pressure level of test signals using an H-52 hydrophone (Groves, 1974), Krohn–Hite filter model 3500, and a Tektronix oscilloscope model 2230. The pool had a skimmer filtering system that does not require pumps. The ambient noise was relatively low and consistent over time, decreasing

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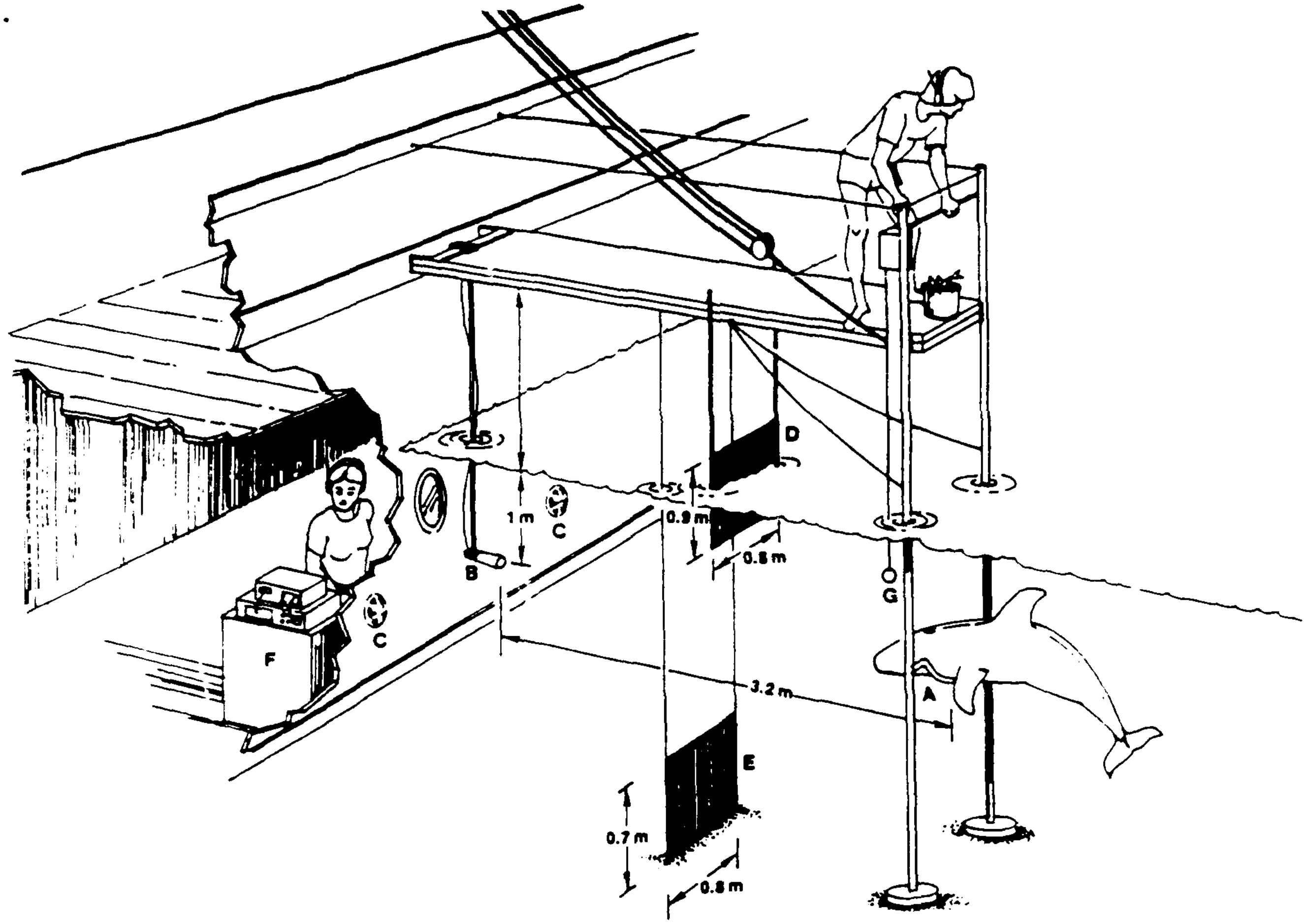

FIG. 1. Diagram of a false killer whale stationed for hearing test: A, crook; B, transducer for projecting test signals; C, underwater lights; D, surface baffle; E, bottom baffle; F, signal-controlling electronics; and G, transducer for projecting training tones.

from 85 dB/(Hz$^{1/2}$) at 2 kHz to 35 dB/(Hz$^{1/2}$) at 115 kHz. The ambient noise of the pool was well below the test signal amplitude at all test frequencies.

Initially, the received level of the test signal at the animal's station exhibited temporal fluctuations of nearly 15 dB for some test frequencies, which most likely were caused by reflections. We designed baffles to block acoustic reflections from the water surface and the pool bottom. Baffles were constructed of 6-mm-thick neoprene rubber glued to a 6-mm-thick aluminum plate and were suspended from the plank between the transducer and the animal. One broke the water surface to interrupt surface reflections (D in Fig. 1) and the other rested on the bottom to damp bottom reflections (E in Fig. 1). The baffles reduced signal fluctuations to 3 dB or less.

C. Stimulus

The trainer on the plank and experimenter in the ship communicated with voice-activated headsets. The signal-controlling equipment was housed below deck (F in Fig. 1), where the experimenter observed the animal's position on station through portholes. A programmable Wavetek function generator (model 172) produced the sinusoidal test signal that was fed to a control box. The control box gated the test signal with a 160-ms rise–fall time and controlled the 2-s duration of the test signal along with the underwater lights. The experimenter selected attenuator settings (in 1-dB steps), the type of trial (signal present or signal absent), and the onset of a trial from the control box. A Tektronix oscilloscope (model T922) monitored the output level to the projector.

Depending on the frequency, we used one of two underwater transducers to project the test signal. Thresholds at 2, 4, 8, 16, 32, 64, 85 kHz were measured using the J9 transducer (Groves, 1974). At 64, 85, 105, 110, and 115 kHz, we used the WAU transducer, a planar four-element (2.7-$\times$2.7-cm aperture), high-frequency transducer constructed by one of the authors.

D. Procedures

The testing regime was a go/no-go response paradigm. The trainer cued the animal to station using a 0.5-s duration 3-kHz tone (G in Fig. 1). When the animal was properly resting on the crook, the experimenter initiated the underwater light/test signal cycle. The underwater lights marked the beginning of a trial and after a 2-s delay, the test signal was projected for 2 s. The lights went off 10 s after the test signal, and a 0.5-s long, 7-kHz release tone signaled the end

of the trial. During a signal-absent trial, the underwater lights went on for 14 s and off as the release tone was given. If the animal detected the test signal, it backed away from the crook immediately (go response). If it did not detect the signal, the whale waited until the trainer gave the release tone (no-go response). The no-go response occurred during signal-absent trials or when the test signal was inaudible.

The trainer used differential reinforcement. The whale received no fish for improper responses, two fish for proper responses to signal-present trials, and four fish for proper responses to signal-absent trials. Because the animal was fed during shows prior to tests, it was unwilling to hold for the 14 s required for signal-absent trials. We controlled this behavior with a greater fish reward during signal-absent trials. This type of reinforcement makes the animal respond conservatively. However, the fish ration during threshold tests was small compared to the whale's daily intake.

Trials were presented using the up/down staircase method (Robinson and Watson, 1973), which results in a 50% correct detection threshold. The experimenter selected trial type (signal present or signal absent) based on a modified Gellerman random series table (Gellerman, 1933). Half the trials were signal absent. We attenuated the signal in 2-dB steps on each signal-present trial until the animal failed to respond to the test signal (miss). We then increased the signal level in 2-dB steps on each signal-present trial until the whale again detected the signal (hit). We designated the transition from miss to hit and hit to miss as reversals. Improper responses to signal-absent trials (false alarms) did not alter the attenuator settings. Trials were repeated until ten reversals were obtained to complete a session. Sessions ranged from 24–69 trials, depending on the consistency of the whale's performance. The order of testing frequencies was random.

The average of the ten reversal points estimated the threshold for a session. When we obtained two consecutive sessions with mean estimated thresholds within 3 dB, we computed the overall threshold for a given frequency. If they were the first two sessions of a new frequency, we continued to collect data until there were another two consecutive sessions with mean estimated thresholds within 3 dB. The criterion for determining high-frequency cutoff was a 120 dB/oct or greater decrease in sensitivity.

II. RESULTS

The stationing crook allowed the animal to move its head freely. During signal-absent or inaudible signal trials, the animal turned and tilted its head (seemingly to optimize signal reception). When we changed to a new frequency, the animal required a few sessions to adjust its head orientation for best reception. Estimated thresholds for each frequency as a function of session order are shown in Fig. 2. Except at 8, 105, and 110 kHz, the whale's threshold indicated progressively greater sensitivity and then stabilized. Using another transducer during the last two sessions at 85 kHz (dashed line in Fig. 2) may have caused the decrease in sensitivity at this frequency; however, a similar trend was not seen at 64 kHz. The hearing sensitivity of this false killer whale compared to audiograms of other cetaceans is presented in Fig. 3.

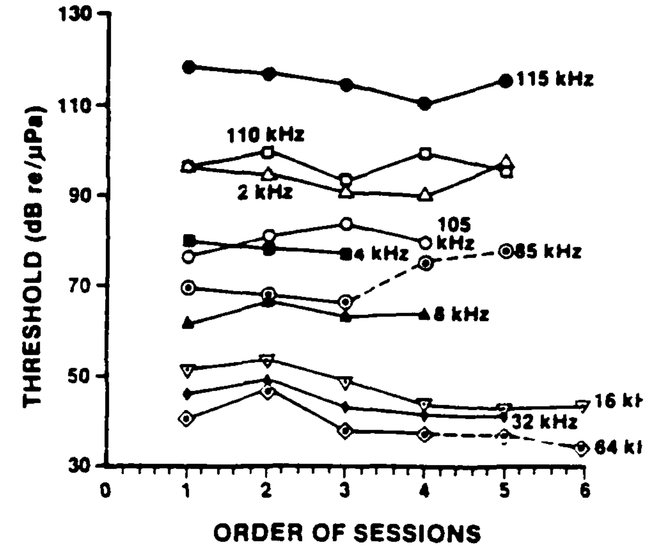

FIG. 2. Summary of estimated thresholds as a function of the order of sions within a frequency. Dashed lines indicate data collected with WAU transducer: all other data were collected with J9 transducer.

The overall threshold and the range of mean session val for each test frequency are presented in Table I. The range greatest sensitivity (defined here as 10 dB from maxim sensitivity) was between 16 and 64 kHz. Below 8 kHz, whale's sensitivity decreased at 38 dB/oct. Above 64 kHz, sensitivity dropped at 150 dB/oct. Our measurements at and 85 kHz were replicated with the J9 and WAU tra ducers; the mean thresholds were less than 3.7 dB apart (T ble I).

We planned to eliminate any sessions with more th 10% false alarms; however, this was not necessary. Fifty-fi percent of the sessions contained no false alarms. Of the maining sessions, the false alarm rate averaged 4% a ranged from 1.9%–9.8%.

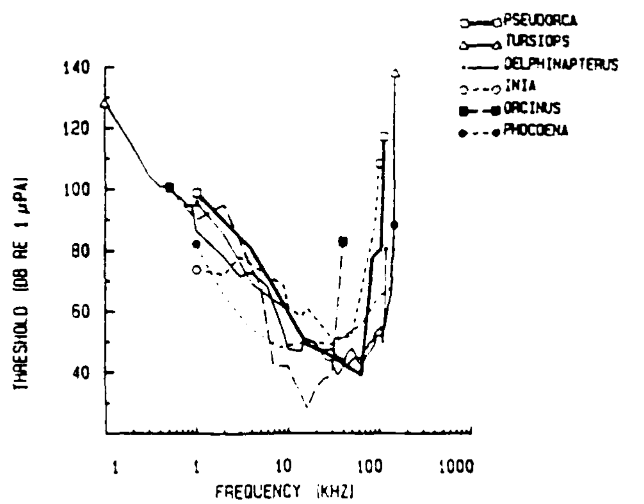

FIG. 3. Comparison of underwater behavioral audiograms from a false k er whale (*Pseudorca*) with those from other odontocetes: harbor porpo *Phocoena* (Andersen, 1970), Amazon River dolphins, *Inia* (Jacobs a Hall, 1972), beluga whales, *Delphinapterus* (White *et al.*, 1978), bott nosed dolphins, *Tursiops* (Johnson, 1967), and killer whales, *Orcinus* (H and Johnson, 1972).

TABLE I. Underwater auditory thresholds of *Pseudorca crassidens* measured with two transducers.

Test frequency (kHz)	Number of reversals tested	Overall threshold in dB re:1 μPa (range of session means) J9 transducer	WAU transducer
2	50	99 (95–101)	
4	30	80 (80–81)	
8	40	64 (62–67)	
16	60	49 (44–55)	
32	50	45 (42–49)	
64	60	39 (38–42)	40 (37–47)
85	50	74 (72–76)	78 (76–79)
105	40		81 (77–84)
110	50		94 (90–98)
115	50		116 (111–119)

We eliminated ten sessions with unstable threshold values because we judged the animal's behavior as atypical from illness or social interactions with pool mates (Table II). The false alarm rates during atypical sessions were not consistently higher than during typical sessions at the same frequency.

III. DISCUSSION

To determine if masking occurred, we need to know the critical ratio and received directivity index for the species. Because these parameters have not been measured for *Pseudorca*, it is difficult to be sure that our threshold measurements were unmasked. However, we used the critical ratio for *Tursiops truncatus* measured by Johnson (1968) and the directivity index reported by Au and Moore (1984) to estimate whether the ambient noise in the pool would mask a *Pseudorca*'s hearing. This comparison showed little probability of masking at any of our test frequencies. The ambient noise in the pool was well below sea state 0 and the quietest available facility for collecting an audiogram.

As shown in Fig. 3, the low-frequency portion of the audiogram of *Pseudorca* (2–8 kHz) is similar to that of *Inia geoffrensis* (Jacobs and Hall, 1972), *Delphinapterus leucas* (White *et al.*, 1978), and *Tursiops truncatus* (Johnson, 1967). Below 4 kHz, *Pseudorca* is as sensitive as *Orcinus orca*. Of all the cetaceans studied, *Phocoena phocoena* (Andersen, 1970) has the most sensitive hearing below 8 kHz.

The audiogram shows that the most sensitive hearing range in *Pseudorca* is between 16 and 64 kHz (10 dB from maximum sensitivity). In this frequency range, *Pseudorca* has approximately the same hearing sensitivity as *Tursiops* and *Delphinapterus* (Fig. 3). Although *Phocoena* and *Inia* are somewhat less sensitive, this also is their best range of hearing. *Orcinus* is more sensitive than other odontocetes from 6–24 kHz and has the narrowest range of peak sensitivity from 12–20 kHz.

The sharp drop in high-frequency sensitivity seems to be a species-specific character in odontocetes (Fig. 3). Sensitivity decreases above 32 kHz in *Orcinus*, above 50 kHz in *Inia*, above 64 kHz in *Pseudorca*, above 120 kHz in *Delphinapterus*, above 140 kHz in *Tursiops*, and beyond 140 kHz in *Phocoena*.

In our study, 10 of 57 sessions (17.5%) had large deviations (± 10 dB) from other thresholds at the same frequency. We identified behavioral correlates for these sessions. It is interesting that during illness or social stress, the animal's responses were inconsistent with other data at the same frequency (Table II). The whale was ill (vomiting) during two sessions (105 and 110 kHz), and the estimated thresholds varied by 18 and 13 dB, respectively, from other sessions at those frequencies. When a bottlenosed dolphin calf was stillborn in the same pool, the whale's estimated threshold was 16 dB less sensitive (Table II). The remaining seven atypical sessions occurred during mid-July/early August (four sessions at 64 kHz and three sessions at 32 kHz). Threshold levels during these seven sessions were 10–25 dB less sensitive. Over time, levels became somewhat more sensitive, but never stabilized. We could not find electrical problems during mid-July/early August. Replicate tests using both transducers in December established greater sensitivity at 32 and 64 kHz and values similar to other cetaceans. According to the animal care staff at Sea Life Park, the whale displayed breeding behavior during this period. We believe that the less sensitive threshold estimates in July/August are related to distraction of our adult male subject during the breeding season. Changes in threshold values during periods of illness or social disturbance may reflect changes in the animal's response criterion, rather than its typical threshold level. However, Table II shows that false alarm rates were not consistently higher during breeding or illness.

Thomas *et al.* (in press) reported that captive *Pseudorca*

TABLE II. Thresholds in μPa and false alarm rates in % for atypical and typical sessions.

Date	Frequency	Atypical sessions Mean false alarm rate	Atypical sessions Mean threshold	Typical sessions Mean false alarm rate	Typical sessions Mean threshold	Animal's behavior
7/18	64 kHz (J9)	5.8%	85 dB	2.9%	40 dB	breeding
7/23		2.1%	78 dB			breeding
7/24		4.2%	76 dB			breeding
7/29		4.0%	76 dB			breeding
8/6	32 kHz (J9)	0%	55 dB	1.4%	45 dB	breeding
8/7		0%	61 dB			breeding
8/8		2.1%	60 dB			breeding
8/13	85 kHz (WAU)	2.4%	61 dB	0%	78 dB	stillborn calf
11/13	105 kHz (WAU)	2.0%	99 dB	1.5%	81 dB	ill
11/26	110 kHz (WAU)	0%	81 dB	1.7%	94.6 dB	ill

produce echolocation pulses with peak frequencies ranging from 20–65 kHz. The peak frequency of echolocation pulses from false killer whales at sea is unknown and could be different than those produced by whales in a reverberant pool. The frequency range of most sensitive hearing in this false killer whale corresponded with the reported peak frequency of echolocation pulses from a captive *Pseudorca*.

IV. CONCLUSIONS

Pseudorca exhibit the typical mammalian U-shaped audiogram. Frequency sensitivity increased gradually from low frequencies to a trough of maximum sensitivity between 16 and 64 kHz (10 dB from maximum sensitivity). High-frequency hearing dropped sharply at a rate of about 150 dB per octave above 64 kHz. Surface and bottom baffles significantly reduced problems with fluctuations in the received level. We believe this contributed to low variation in estimated thresholds among sessions. We suggest that careful records of environmental and social influences may help interpret seemingly atypical threshold levels. The range of greatest hearing sensitivity in this false killer whale corresponded with the peak frequency of echolocation pulses from a captive *Pseudorca*.

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